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## **Behaviour and EEG of drowsy and sleeping cats**

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## SUMMARY

The correlation between spontaneous sleep behaviour and EEG was studied in four intact, freely moving, adult domestic cats.

Current concepts of this correlation, derived from a descriptive, qualitative approach, can be briefly summarized as follows. The range from alert wakefulness to deep sleep has been divided into stages on the basis of the observed coincidence of specific behaviour patterns and specific EEG patterns. Classified according to "depth of sleep", these stages are: I. alert wakefulness, II. relaxed wakefulness, III. light sleep, IV. intermediate sleep, V. rapid eye movement sleep (REM). Relaxed wakefulness, light sleep and intermediate sleep are not strictly defined entities, either in behavioural or in electroencephalographic respects. The transitions between these stages are often described as gradual and continuous. In fact, a number of authors distinguish two instead of three stages. The various EEG patterns accompanying the three stages are frequently referred to as the "synchronized EEGs", the extent of synchronization being a measure of the "sleep depth".

The remaining stages, alert wakefulness and REM sleep, are characterized by EEGs which are generally believed to be identical: the "desynchronized" EEGs. Behaviour during the REM sleep can be clearly distinguished from that in each of the other stages, still there are many reasons for regarding it as sleep behaviour. Hence, the paradoxical situation exists that clear-cut sleep behaviour is accompanied by an EEG otherwise encountered only in alert wakefulness. Because of this, as well as because of numerous peculiarities in other respects, REM sleep has been given a rather exceptional and much disputed position among the sleep stages. There are therefore differing views on the "depth" of sleep in this stage. Its placement under V. in the outline presented above, suggesting that REM sleep would be the "deepest" stage of sleep, reflects the opinion of only a limited number of authors. Current concepts are often neutrally formulated in the summarizing statement that two kinds of sleep exist: "synchronized sleep" and "desynchronized sleep".

In contrast to previous investigations, this report presents an objective and quantitative analysis of behaviour, EEG and their interrelations.

### Behaviour

The following motor phenomena were observed: the body posture (sitting, crouching, sphynxing or lying), the position of the head (upright, lowered or dropped on the ground) and the width of the opening of the

eyelids (open, half open, a quarter open or closed). The observer was ignorant of the EEG simultaneously recorded.

The observation records (covering time spans of about one hour) revealed that there were sequential periods during each of which none of the above mentioned behaviour elements changed. Such stable combinations of elements were called behavioural states. It is apparent from the results of the observation of behaviour that the process of the onset of sleep is stepwise, the behavioural states being the "stepping stones". This suggests that the underlying mechanisms may also be stepwise, rather than gradual and continuous.

Of the theoretically possible number of combinations of behaviour elements only a limited number occurred, indicating that the behaviour elements studied are interrelated in a specific way.

Furthermore, considerable differences were found between individual cats concerning the kinds of behavioural states displayed.

The above mentioned behavioural findings have partly determined the methods employed in correlating behaviour and EEG.

## **Behaviour and EEG**

Simultaneously with the observation of behaviour, EEGs were recorded on paper and on magnetic tape. The fronto-parietal records were analyzed afterwards with an automatic frequency analyser.

The results of the observation of behaviour were the starting point for the examination of the electroencephalographic data. As the behaviour elements observed showed specific relationships with each other, investigation was first made of the correlation between the combinations of these elements and the EEG. Thus behavioural states and not just single behavioural elements were correlated with EEG. Because of individual differences in behaviour, the correlation of behaviour and EEG was examined for each cat separately.

Comparison of the observation records, the EEGs and the frequency analyses showed that each behavioural state was accompanied by a variable EEG. The variability was evident in a number of respects. Visual judgement of the EEG, employing the conventional criteria described in the literature, by electroencephalographers who did not know either the concomitant behaviour or the frequency analysis, frequently resulted in the finding of more than one sleep pattern per behavioural state. In other words, stable non changing behaviour (as defined in the present study) might be accompanied by more than one electroencephalographic sleep stage. But even when one particular state was accompanied by one particular EEG pattern, the write-out of the frequency analyser showed an

enormous variability with respect to amplitude and frequency spectrum.

Accepting the fact of EEG variability during periods of stable behaviour, the question arose as to whether this very variability would differ from one behavioural state to another. To determine one aspect of EEG variability the relationship was examined between voltage and frequency spectrum. The quantitative data were computed from the measurements made by the automatic analyser. All periods during which a particular behavioural state was displayed were sampled from the observation records and the relationship between voltage and spectrum of the concomitant EEGs was determined. This was done for all behavioural states.

The investigations revealed that the EEGs of all cats display two types of variability, called A and B. Each of these is correlated with one coherent complex of behavioural states.

In type A voltage and frequency spectrum are correlated as follows: Whenever the EEG voltage increases, the peak of the frequency spectrum shifts towards the lower frequencies; likewise, whenever the voltage decreases, the higher frequencies become more dominant.

In type B a different correlation between voltage and frequency spectrum exists: although the voltage of these EEGs may vary extensively, the frequency spectrum always shows the same predominance of the low frequencies.

Since the correlations are high, it may be concluded that the relationship between voltage and frequency spectrum is regulated accurately.

In between the two complexes of behavioural states characterized by type A and type B EEG variabilities, there remains a third coherent complex. The EEGs associated with the behavioural states belonging to this complex, showed EEG variability of either type A or type B.

This distribution of the types of variability over the behavioural states demonstrates the close connection between the behavioural and electroencephalographic variables. More detailed investigation of this distribution shows that, of the three behaviour elements, the width of the opening of the eyelids is likely to be the most important one in determining the correlation between behavioural state and type of EEG. The type B variability is almost exclusively found when the eyes are closed, although the body posture and the position of the head may then vary. This suggests that closure of the eyes is the prominent factor. On the other hand, since the range of variation of body posture and head position is very limited when the eyes are closed, it is clear that the width of the opening of the eyelids is not the only factor: all the behavioural elements contribute to the picture with relative, different weights. This interdependence of behaviour elements can be further demonstrated by the fact that, for instance, the width "eyes a quarter open" in combination

with certain body postures and head positions may be accompanied exclusively by EEGs with the type A variability, whereas combinations with other body postures and head positions may be associated with EEGs with the type B variability as well.

### REM sleep

Visual comparison of EEGs recorded during REM sleep with the EEG of alert wakefulness does not reveal differences. Automatic frequency analysis of these EEGs, however, shows marked differences. In the EEGs accompanying alertness the high frequencies dominate, whereas in the EEGs of REM sleep mainly low frequencies are found. This difference becomes visually evident when the two kinds of EEGs are amplified.

Correlation of voltage and frequency spectrum in the two EEGs demonstrates that the variability of the EEG of alert wakefulness has the characteristics of type A. The variability of the EEG accompanying REM sleep has the features of type B.

The question arose whether the low voltage EEG of the REM sleep might be a very much reduced specimen of the high voltage slow activity EEG of "intermediate sleep" which shows the variability of type B. Amplification of the EEG of REM sleep to the voltage level of "intermediate sleep EEGs", and comparison of the amplified signal with the unamplified type B EEGs, provides no clear answer to this question. Although similarities in the two EEGs can be noted, morphological differences exist as well. This suggests that the EEG of REM sleep cannot be simply a reduced high voltage slow activity EEG. Visual inspection and frequency analysis suggest that the two types of EEG consist of the same components, but that the seriation (the "grouping") of these components differs in each of them.

### Relation of the findings to current concepts

It is clear that, when analyzed according to the method described, the electroencephalographic, and to a large extent also the behavioural phenomena, fall into two groups. One cluster in the sleep behaviour is correlated with one type of EEG variability, a second cluster is accompanied by a second type of EEG variability, and the remaining intermediate cluster provides EEGs either of the first or of the second type of variability.

The question arose as to the nature of the relation between the conventional behavioural and electroencephalographic categories, and the categories proposed in the present study. To what extent do the different sets of categories coincide, and in what respects do they differ? This problem was

not studied extensively and will be an issue for future research. Some remarks on the nature of this relation can, however, be made already with reasonable certainty.

The EEGs with variability of type A cover the EEG patterns usually ascribed to alert wakefulness (I) and part of the patterns of relaxed wakefulness (II). This means that a "desynchronized" EEG (I) and a "synchronized" EEG (II) fall into one category. (See for these and following remarks (fig. 73).

The EEGs with variability of type B comprise the EEGs ascribed to intermediate sleep (IV) and the EEGs of REM sleep (V). Thus, again a "synchronized" EEG (IV) and a "desynchronized" EEG (V) go together in one category.

As regards the EEG of the stage "light sleep" (III), the position is not clear. While some data indicate that this EEG probably belongs to the type B category, the possibility remains that part of these EEGs also belongs to the type A category.

Whatever conclusions will ultimately be drawn, it is already clear that the gross distinction between EEGs with type A and those with type B variability by no means coincides with the usual gross distinction between "synchronized" and "desynchronized" EEGs.

Many concepts concerning the physiological mechanisms underlying sleep and the neuroanatomical substrates involved are based on data which are reported and interpreted in the literature in terms of "synchrony" and "desynchrony". These categories do not coincide with those presented here. Furthermore, the descriptions of behavioural findings are often reported in terms of sleep stages, thus rendering translation into behavioural states difficult. It will be clear that these divergences to a large extent handicap attempts to relate the findings of the present study with current theories and speculations on the mechanisms of sleep. A number of data previously reported in the literature indicate, however, that the dichotomy in sleep phenomena introduced here, may be meaningful and relevant in behavioural, neurophysiological and neuroanatomical respects.